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► To cite this version:

Pieter de Frenne, Florian Zellweger, Francisco Rodríguez-Sánchez, Brett Scheffers, Kristoffer Hylander, et al.. Global buffering of temperatures under forest canopies. Nature Ecology & Evolution, 2019, 3 (5), pp.744-749. 10.1038/s41559-019-0842-1. hal-02352625

HAL Id: hal-02352625 https://hal.science/hal-02352625

Submitted on 13 Nov 2019

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Global buffering of temperatures under forest canopies

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24 Abstract

25	Macroclimate warming is often assumed to occur within forests despite the potential for tree cover
26	to modify microclimates. Using paired measurements (under the canopy vs. in the open) at 98 sites
27	across five continents, we show that forests function as a thermal insulator, cooling the understory
28	when ambient temperatures are hot and warming when ambient temperatures are cold. The
29	understory vs. open temperature offset is magnified as temperatures become more extreme and is of
30	greater magnitude than the warming of land temperatures over the past century. Tree canopies may
31	thus reduce the severity of warming impacts on forest biodiversity and functioning.

32 Main text

33	Biological impacts of macroclimate warming are increasingly evident across a wide array of
34	ecosystems ¹⁻⁵ . Many responses of biological communities and ecosystem processes, however, are
35	lagging behind warming of the macroclimate ⁶⁻¹¹ . Such time lags may be the inevitable consequence
36	of slow dispersal and demography ^{3, 7, 8} , but may also be due to the buffering of localized
37	microclimates by vegetation and topography, such that organisms do not necessarily experience the
38	same degree of warming as measured at weather stations ¹²⁻¹⁸ . Biotic and abiotic features near the
39	ground create heterogeneous microclimates, mostly via effects on radiation, air mixing,
40	evapotranspiration and soil properties, all of which can influence biodiversity and ecosystem
41	functioning ^{17, 18} .
42	To better predict the biotic consequences of climate change, we need to further our
43	understanding of how the local temperature experienced by living organisms (referred to as the
44	'microclimate') changes in space and time. Macroclimates outside forests (sometimes referred to as
45	'free-air temperatures' in the literature) are characterized by an extensive global network of weather
46	stations established in the well-mixed air of open areas (e.g. short grasslands) c. 2 m above the soil
47	surface ^{19, 20} — habitat conditions that are not representative of the conditions experienced by the
48	majority of terrestrial species on Earth ^{21, 22} . The study of microclimates is not new, since
49	microclimatological measurements began more than a century ago, but most climate-change studies
50	rely on weather station data that are specifically designed to correct for these microclimatic effects ¹⁵⁻
51	²⁰ . Hence, future projections of climate change relying solely on macroclimate ignore the potential
52	impact of microclimates on biodiversity and ecosystem functioning ^{1, 2, 5} .
53	Microclimates are particularly evident in forests, where the large majority of species live

54 underneath the canopy of trees that strongly influences local thermal conditions¹⁰⁻¹³. This is of major

55	concern for global-change science because forests cover one-quarter of the Earth's land surface and
56	harbor two-thirds of all terrestrial biodiversity ²⁰⁻²³ , and some studies have already shown that
57	microclimatic buffering can mediate the response of forest communities to climate change ⁸⁻¹¹ .
58	Here we report a systematic, global meta-analysis quantifying the thermal buffering capacity of
59	the Earth's dominant forested ecosystems (tropical to boreal forests) across five continents (Fig. 1).
60	Drawing on empirical studies with a strictly paired design (i.e. comparing microclimate with
61	macroclimate), we quantify the average temperature offset of forests and also how the magnitude of
62	such offsets depends on the macroclimatic context (i.e. outside forests). From a total of 98 sites and
63	74 studies, we retrieved paired temperature time series and/or summary statistics (i.e. minimum,
64	mean, or maximum temperatures) for exactly the same time period in (i) understory conditions in
65	forests (i.e. microclimate) and (ii) an adjacent open habitat without shade (i.e. macroclimate). Offset
66	values were always calculated as temperatures inside minus macroclimate temperatures outside
67	forests such that negative values reflect cooler forest temperatures.
68	In our global analysis of 714 paired temperature data, we found that tree canopies buffer
69	forest floors against both high and low macroclimatic temperatures. Mean and maximum understory
70	temperatures were, on average, cooler by 1.7 \pm 0.3 and 4.1 \pm 0.5 °C (mean \pm S.E., mixed-effects
71	models: both $P < 0.001$) than macroclimate temperatures, respectively. Conversely, minimum
72	temperatures of the forest understory were 1.1 \pm 0.2 °C warmer than the macroclimate outside the
73	forest (mixed-effects model: $P < 0.001$; Fig. 1, Supplementary Figs. 1-2). Thus, forest understories
74	are not only cooler on average than nearby open habitats, but negative maximum temperature
75	offsets (cooler in forests) and positive minimum temperature offsets (warmer in forests) also
76	indicate lower temperature variation below the forest canopy.

77	Across the globe, the thermal offset of forests was negatively correlated with the macroclimate
78	temperature outside forests. Thermal offsets became more negative (i.e. lower temperatures in
79	forests) as macroclimate temperature increased, and more positive (i.e. higher temperatures in
80	forests) as macroclimate temperature decreased (Fig. 2a, Supplementary Figs. 3-4). The cooling of
81	mean and maximum temperatures was highest in tropical forests (probably partly as a result of the
82	latitudinal gradient in macroclimate temperatures; Fig. 2a) while minimum temperatures were highest
83	in boreal forests, relative to the macroclimate temperature (Fig. 2b). This means that the latitudinal
84	gradient of forest-floor temperatures is less steep than the latitudinal gradient in macroclimate
85	temperature and that the amplitude of change within a given microhabitat does not always equate to
86	the amplitude of macroclimate change ¹¹ .
87	To control for the effects of spatiotemporal changes in macroclimate temperatures (e.g.
88	sampling of tropical vs. boreal forests, low vs. high elevations or warm vs. cold years) on the
89	magnitude of the offset, we computed macroclimate temperature anomalies relative to the average
90	conditions over the period 1970-2000 for each of the 98 study sites, and subsequently used it as a
91	predictor variable instead of actual temperatures outside the forest reported in the original studies.
92	The results are in line with those using raw temperature values rather than anomalies: the cooling
93	effect on maximum and mean temperatures, as well as the warming effect on minimum
94	temperatures, are consistent along the gradient of temperature anomalies, with very similar slope
95	estimates compared to the models with actual macroclimate temperatures (Supplementary Fig. 5).
96	Together, these results suggest that the thermal offsetting capacity of forests across the globe
97	may translate into lower warming in the forest understory compared to warming trends using
98	weather-station data from non-forested areas. Forests across the globe are thus effectively serving as
99	a thermal insulator compared with open areas, with such a buffering effect potentially reducing the

severity of climate change impacts on forest ecosystems. The offset values we report here now have
 to be compared to the thermal sensitivities of species and ecosystem processes to better predict
 ecological responses to increasing temperatures.

103 In addition to spatiotemporal variability, we also tested for additional factors that might 104 explain some of the variation among studies in the magnitude of temperature offsets, such as forest 105 composition (evergreen, mixed or deciduous), tree height, topography, distance to the coast, or the 106 height of the temperature sensors (e.g. aboveground or belowground) (Supplementary Figs. 6-7; 107 Supplementary Table 5). Sensor height indeed impacted the magnitude of the offset: the buffering in 108 forests was strongest close to the ground while the difference in temperatures between forests and 109 open habitats disappeared higher up above-ground, both for minimum and maximum temperatures 110 (Supplementary Fig. 7). Contrary to what we expected based on the scientific literature²⁴, we did not 111 detect an effect of the type of dominant tree species (evergreen, deciduous or mixed), topography, 112 distance to the coast or forest height on the offset; more targeted studies will be needed to provide stronger tests of such factors. 113

114 Paleoecological records show that temperature changes of greater magnitude and rate have stronger biological consequences^{5, 25}. Here we have shown that microclimate buffering in forests has 115 116 the potential to partly offset the warming experienced in the forest understory due to anthropogenic 117 climate change, effectively reducing the severity of impacts from heating of the atmosphere. As such, closed forest canopies might provide a line of defense against the impacts of current and 118 119 future warming on the ecological processes that influence forest ecosystems (e.g. tree regeneration, 120 demography and community reshuffling, litter decomposition, and soil water and nutrient cycling). 121 In addition, because offsetting was strongest for maximum temperatures, we might expect extreme 122 events such as heat waves to be more strongly attenuated than gradual temperature changes.

123	Our results underpin a neglected function of forests: an offset of within-forest temperatures
124	that is of greater magnitude than the global warming of land and ocean temperatures over the past
125	century (~0.85 °C, ref. 4) and also the warming of regional surface temperatures following
126	deforestation (usually \leq 1 °C, ref. 26). Forest canopies serve as thermal insulating layers, likely
127	offsetting the impacts of anthropogenic climate change in the understory, where a large share of
128	forest biodiversity resides and key ecosystem processes take place ^{21, 22} . It is thus essential to
129	incorporate microclimates into biodiversity and climate science as well as into forest management
130	and policy. As forest loss, degradation, and conversion to monoculture crops continues ^{27, 28} , human
131	land use might undermine ecosystems' natural ability to mediate climate warming (a positive
132	feedback). Such feedbacks to climate systems may be further exacerbated via effects of
133	microclimates on soil CO ₂ and CH ₄ fluxes and sub-canopy evapotranspiration rates ²⁹ .
134	Advances in studies of micro- vs. macroclimate change have thus far been limited by the
135	availability of suitable spatial data to model and map small-scale heterogeneity of microclimate
136	conditions ^{10-17,24} . Our global analysis shows the importance of forests in moderating climate
137	warming, and the next step will be to incorporate fine-grained thermal variability into bioclimatic
138	modelling of future species demography and distributions ¹⁴⁻¹⁷ . Our findings indicate that well-
139	quantified microclimates are key to improving predictions of climate-change impacts and assisting
140	management decisions. Forest managers and policy makers alike can potentially exploit microclimate
141	buffering as a regulating service when developing mitigation and adaptation plans to safeguard forest
142	biodiversity and functioning as well as human well-being in a future, warmer world.

143 Methods

144 Literature search and data extraction

We performed a literature search on ISI Web of Science to compile suitable published studies 145 146 assessing the thermal offsetting capacity of forest ecosystems. This search was updated until 15 June 147 2017 and performed by each of three authors (PDF, FZ, JL) independently, using keywords such as microclimat*, microrefug*, microhabitat*, forest*, temperature* and buffer*. The combined number 148 149 of potentially suitable papers found by these three independent searches was 706. We then screened the titles and abstracts to find studies that potentially met our requirements for data extraction (see 150 151 the next paragraph). We considered forest microclimates to represent the suite of climatic conditions measured in localized areas near the ground and within the forest understory (below tree canopies). 152 153 Microclimatic conditions include temperature, precipitation, wind and humidity, but the focus here 154 was on the temperature of the air layer below tree canopies and the temperature of the topsoil due 155 to their importance for the responses of forest organisms and ecosystem functioning to 156 macroclimate warming. The macroclimate was considered as the climate in free-air conditions, 157 representative of a large geographic region without direct canopy effects. This definition follows the 158 definition used by meteorologists who record synoptic or macroclimate conditions from standardized weather stations¹⁹⁻²⁰. 159

Our criteria for study inclusion were the following: studies had to report temperature values (time series or summary statistics such as minimum, mean or maximum values) according to a strictly paired design comparing microclimate below trees (inside forests) with temperatures recorded from a reference neighbouring site outside the forest without any influence of trees (i.e. macroclimate conditions). Reference sites were either a nearby open site equipped with the same type of (shielded) temperature loggers, a nearby weather station (as long as the distance did not confound with the temperature offset of the canopy, e.g. due to significant topographic differences), 167 or a logger placed above the upper canopy surface. Constancy of the location of temperature sensors 168 within a pair of observations (e.g. forest soil temperatures were only compared with control soil temperatures) was a requirement. Temperature data presented in tables or text were entered directly 169 170 into our database. Temperature data not available directly in the text, raw data or as tables but presented in figures in the original papers (42.3 % of the total number of offset values) were 171 172 extracted using the digitalization software *WebPlotDigitizer* 173 (https://automeris.io/WebPlotDigitizer/). We did not set any limit on the study duration, i.e. we 174 extracted data from studies that quantified paired temperature time series during single days up to 175 several years. If studies were performed along an edge-to-core transect, we only considered the 176 measurements outside the forest farthest away from the edge versus the measurement closest to the 177 core of the forest (as far away from the edge as possible). We screened the titles and abstracts of all above-mentioned 706 publications. In addition, we included a formal process of scanning references 178 179 lists of relevant papers and further added potentially relevant papers extracted from these reference lists. In total, we identified 74 studies published between 1939 and 2017 that met our above-180 mentioned requirements for data extraction. The majority of the studies were reported in peer 181 182 reviewed journal articles, but also 2 PhD theses, 1 book and 2 institutional reports were included.

183 When raw temperature data were available, we computed three summary statistics: maximum, 184 mean and minimum temperatures across time. If available, we extracted temperatures outside and 185 inside the forest and then calculated the magnitude of the offset as understory temperature minus 186 temperature outside the forest; negative values thus reflect cooler temperatures below tree canopies 187 while positive values reflect warmer understory temperatures. A third of the studies (34 % of offset 188 values) only reported the macroclimate vs. understory temperature difference (and not the forest and 189 macroclimate temperatures separately). In these instances, only the offset value itself was directly 190 entered in our database. Replicate forest sites (at least several kilometers apart), seasons

(meteorological seasons, later aggregated to growing vs. non-growing season) and temperature
 metrics (maximum, mean, minimum, air or soil temperatures) within the same study were entered on
 different rows into the database. Temperature values of longer time series were always aggregated
 per season and/or year.

All authors contributed to the data extraction from the original papers. After the first data extraction, however, all entries into the database were thoroughly double-checked by four authors (PDF, FZ, FRS, JL), working together closely to resolve any discrepancies or ambiguities and to ensure a standardized protocol across all papers. We used the following R packages for data management, cleaning and visualization: readxl³⁰, dplyr³¹, CoordinateCleaner³², knitr³³, rmarkdown³⁴, ggplot2³⁵, and cowplot³⁶, as well as custom R code³⁷.

- In total, our final database consisted of 714 paired temperature offset data points from 74 independent studies spread across five continents. Our full database with all variables used in the analyses, as well as all source code, is reported in ref. 37.
- 204

205 <u>Predictor variables</u>

Apart from the temperature variables, we also extracted the following attributes for each offset valueand/or study, if available in the original source article:

208 • Location: Latitude
209 • Biome: Based or
210 following three
211 (latitude was bety

• *Location*: Latitude, longitude and elevation (meters above sea level).

• *Biome*: Based on the geographical coordinates, we classified each site into one of the following three biomes: tropical (latitude was between 23.5°S and 23.5°N); temperate (latitude was between 23.5° and 55°); or boreal (latitude was higher than 55°).

- *Vegetation type:* Based on the original source article, or, if needed, additional sources (e.g. other papers from the same study site and/or authors), the forest type was classified into each of three categories: deciduous (if dominant tree species was deciduous; 1 in dataset via ref. 37); evergreen (if dominant tree species was evergreen; 2); or mixed (3).
- Study length: number of days during which temperatures were measured, ranging from 1 day
 to 10 years.
- Forest density: We extracted for each study site, if available, any of the following variables
 relating to forest density: canopy cover (%); tree basal area (m² ha⁻¹); tree density (number ha⁻¹); and leaf area index (LAI). Each of the above-described variables was available for a
 minority of offset values: 16 % for canopy cover, 23 % for basal area, 7 % for tree density
 and 8 % for LAI. For reasons of paucity of these data, we do not consider these variables
 further in our analyses, but the raw data are available in ref. 37.
- *Forest height*: We extracted for each study site, if available (39 % of offset values), the height
 of the dominant tree individuals (in meters).
- 226 Topographic heterogeneity and distance to the coast: because of known effects of topography²⁴ on • 227 microclimates, we also extracted topographic heterogeneity using raster layers derived from 228 the Global Multi-resolution Terrain Elevation Data 2010 (GMTED2010) at 250 m resolution³⁸. We here focused on two variables that capture topographic heterogeneity within 229 230 a 1 km² pixel around each pair of measurements (forest and macroclimate outside forest): (i) 231 the standard deviation of elevation values aggregated per 1 km² (further referred to as 'elevational variation'), and (ii) the median of the topographic position index (TPI) values at 232 233 1 km resolution. The TPI is the difference between the elevation of a focal cell and the mean 234 of its eight surrounding cells. Positive and negative values correspond to ridges and valleys, respectively, while zero values correspond to flat areas³⁸. Finally, we also extracted the 235

distance from each pair of measurements (forest and macroclimate outside forest) to thenearest coastline.

Season of sampling: Temperature measurements were classified as having taken place during
 the growing season, the non-growing season, or whether the whole year was sampled
 (annual). This was aggregated based on reported meteorological seasons and/or climate
 information in the original study. The dry and winter season were classified as the non growing season in tropical and temperate biomes, respectively.

- Height of the sensor (continuous variable, in meters above or below the soil surface): positive
 for aboveground, negative for belowground sensors. While soil temperatures obviously do
 not reflect macroclimate temperatures, they still allow for a comparison of forests' thermal
 buffering capacity on soil organisms and processes. The effects of macroclimate
 temperatures on the offset were similar when only considering sensors placed > 0 cm above
 the soil surface.
- 249 Macroclimate temperature anomalies: We calculated the difference between each macroclimate • 250 temperature and the long-term average temperature for a given site. This was done in order 251 to test if the increase in temperature offset with warmer macroclimate temperatures was due 252 in part to temporal variation in macroclimate, rather than only spatial variation. 253 Macroclimate temperatures are thus compared to a common baseline. Using these 254 temperature anomalies, we asked how the magnitude of the thermal offset capacity of forests 255 varies along a gradient of deviations from long-term temperature averages, analogous to 256 IPCC definitions of climate change⁴. We used 1970-2000 as reference period to compare our macroclimate temperatures outside forests against a common base period. Location-specific 257 long-term averages (1970-2000) of mean annual temperatures were extracted from 258

259 WorldClim version 2 at 30 arc-second spatial resolution (approximately equivalent to 0.86
260 km² at the equator) for each study site³⁹.

261

262 Data analyses

263 To report summary statistics of the thermal offset capacity of forests globally (Supplementary Table 1), two contrasting approaches were adopted. First, the raw mean, median and quantiles were 264 265 calculated. Then, we carried out a multilevel modeling framework using intercept-only linear mixedeffects models (LMMs) without fixed predictor variables but with 'study' as a random intercept term 266 to account for pseudo-replication in some of the 74 selected studies. The intercept of intercept-only 267 268 models represents the average magnitude of the thermal offset of forests while accounting for the 269 non-independence among replicates from the same study. When fitting our intercept-only LMMs, we used the restricted maximum likelihood method in the *lmer* function from the *lme4*-package⁴⁰ as 270 recommended by Zuur et al.⁴¹. 271

Applying a conventional meta-analytical model *sensu stricto* with weighting of different observations by means of variance estimates⁴² was not possible here: an estimate of uncertainty (standard error, deviation, coefficient of variation or confidence intervals) of the offset values was reported for only a small minority (13.6 %) of offset values included in our database.

276 Next, we assessed how macroclimate temperatures and macroclimate temperature anomalies 277 predicted variation in the temperature offset of forests globally. As above, we fitted LMMs with 278 macroclimate temperatures and macroclimate temperature anomalies as fixed effects and '*study*' as a 279 random effect using restricted maximum likelihood in the *lmer* function from the *lme4*-package⁴⁰. We 280 also performed χ^2 -tests by comparing the univariate LMM including a single predictor with the baseline intercept-only model⁴¹. Goodness-of-fit was determined by calculating marginal and
 conditional R² values following ref. 43 using the *r.squaredGLMM* function in the *MuMIn*-package⁴⁴.

283 We also determined how variables such as absolute latitude, biome, elevation, vegetation type, 284 distance to the coast, the elevational variation and topographic position, season, and sensor height influenced variation in the offset of forests, and how they interacted with macroclimate 285 286 temperatures. We first ran seven separate univariate LMMs, one per predictor variable as a fixed effect in our LMMs. As earlier, we again fitted LMMs with a random effect term 'study' using 287 restricted maximum likelihood in the *lmer* function from the *lme4*-package⁴⁰. In order to test 288 interactions, we finally also ran LMMs with two predictor variables each: the macroclimate 289 temperature and each of these seven other predictors (i.e. one-by-one of these seven variables * 290 291 macroclimate temperature); for the sake of simplicity, higher level interactions were not considered (Supplementary Table 6). 292

293 Finally, the linearity of the relationship between the temperature offset and macroclimate temperatures was tested with General Additive Mixed Models with the gamm-function in the mgcv-294 package⁴⁵ and again *study* was added as random term (Supplementary Fig. 4). Our main findings were 295 296 robust to the decisions to (i) analyze understory temperatures as the response variable against macroclimate temperature as a fixed effect in LMMs, instead of intercept-only LMMs based on 297 offset values (Supplementary Fig. 3), and (ii) add random intercepts into LMMs, instead of random 298 slopes (Supplementary Table 7). Omitting a few outlier values from a single study¹²⁰ from the 299 300 analyses also did not affect our conclusions (Supplementary Table 8).

All analyses were performed in R version 3.4.4 (ref. 46) and all retained papers are in the
 reference list⁴⁷⁻¹²⁰. All raw data and code are available in ref. 37. Full results of the statistical analyses
 are reported in Supplementary Tables 1-8. We followed best practices for reporting meta-analyses

recommended by the PRISMA guidelines¹²¹ and included a flow diagram summarising the search
criteria in Supplementary Fig. 8.

306 Acknowledgements

- 307 PDF received funding from the European Research Council (ERC) under the European Union's
- 308 Horizon 2020 research and innovation programme (ERC Starting Grant FORMICA 757833), KV
- 309through ERC Consolidator Grant PASTFORWARD 614839, FRS by a postdoctoral fellowship
- 310from the Spanish Ministry of Economy and Competitiveness (FPD-2013-16756), FZ by the Swiss
- 311 National Science Foundation (project 172198) and MV by the Natural Sciences and Engineering
- **312** Research Council, Canada.

313 Author contributions

PDF, FZ and JL conceived and designed research. PDF, FZ, JL and FRS assembled and revised thedatabase, and analyzed the data. All authors compiled data and wrote the manuscript.

316 Competing interests

317 The authors declare no competing interests.

318 Materials and Correspondence

319 Correspondence and requests for materials should be addressed to P.D.F.

320 Data availability

- 321 The datasets and code generated and analysed during the current study are available in the figshare
- repository³⁷, with the identifier 10.6084/m9.figshare.7604849

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589 Figure Legends

590 Fig. 1 | Forests buffer temperatures under canopies globally. a, Distribution of the 98 study 591 sites and their vegetation type (deciduous, evergreen or mixed forests). b, Histograms display the 714 paired temperature offset values for maximum (T_{max}), mean (T_{mean}) and minimum (T_{min}) 592 temperatures. Maximum and mean temperatures are consistently cooler, and minimum temperatures 593 594 consistently warmer, within forests compared to macroclimate temperatures. Offsets were always calculated as temperatures inside minus macroclimate temperatures outside the forest such that 595 596 negative (positive) values reflect cooler (warmer) forest temperatures. Offset means and standard 597 errors are based on mixed-effects models with study as a random-effect term. Full statistical 598 analyses, data and code are reported in Supplementary Information and ref. 37.

599 Fig. 2 | Forest temperature offsets under canopies are negatively related to warming air 600 temperatures and dependent on the biome. a, The magnitude of the temperature offset within forests depends on ambient macroclimate temperature: the higher the warming, the more offsetting 601 602 of temperatures (T_{max} and T_{mean}). For minimum temperatures, positive offsets increase with colder 603 temperatures. **b**, Study sites were classified into boreal, temperate or tropical, based on their latitude. Offset values were always calculated as temperatures inside minus macroclimate temperatures 604 605 outside the forest such that negative (positive) values reflect cooler (warmer) forest temperatures. Regression slopes, 95% confidence intervals (grey shading), and offset means (red lines), are based 606 607 on mixed-effects models with study as a random-effect term. Full statistical analyses, data and code 608 are reported in Supplementary Information and ref. 37.

a



Fig. 2 | Forest temperature offsets under canopies are negatively related to warming air
temperatures and dependent on the biome

